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# SIZE- AND DIET-RELATED VARIATIONS IN ENZYMIC ACTIVITY AND TISSUE COMPOSITION IN THE SABLEFISH, *ANOPLOPOMA FIMBRIA*

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## Abstract

The influences of body size, ration size, season, and latitude on several biochemical properties of skeletal muscle and liver were examined in the sablefish, *Anoplopoma fimbria,* to understand how these factors interact to establish the biochemical and physiological condition of the organism. Activities in muscle of the glycolytic enzymes lactate dehydrogenase (LDH) and pyruvate kinase (PK) increased significantly with increasing body size. This size-dependent variation in enzymic activity must be corrected for when the effects of other enzyme activity influencing variables, *e.g.,* ration size, are studied. Ration size had a strong influence on muscle enzyme activities and on the water and lipid content of muscle. Starvation led to large decreases in glycolytic enzyme activity and lipid content. The LDH content of muscle was directly proportional to the amount of food ingested (expressed as percent body weight ingested per day). Latitudinal differences among sablefish collected between Alaska (Bering Sea) and southern California and seasonal differences among individuals collected off southern California also may be due to varying ration quantity and quality. During starvation, lipid reserves in muscle appear to be mobilized as a major energy source in preference to protein.

## Introduction

Recent studies of marine teleost fishes have shown that certain biochemical characteristics of white skeletal muscle, notably enzymic activity (expressed as units per gram wet weight) and protein content, correlate strongly with important ecological and physiological attributes of the species. Comparisons of species having different depths of occurrence have shown that the activities of two glycolytic enzymes (lactate dehydrogenase [LDH] and pyruvate kinase [PK]) decrease by two to three orders of magnitude with increasing depth of occurrence (Childress and Somero, 1979, Sullivan and Somero, 1980; Siebenaller and Somero, 1982; Siebenaller *et al.,* 1982). Because LDH and PK activities reflect the capacity of a fish for vigorous high speed swimming (Somero and Childress, 1980; Sullivan and Somero, 1980), these depth-related changes in glycolytic activity are interpreted to reflect greatly reduced locomotory capacities in deeper-living fishes. Several differences in LDH and PK activity were also found among fishes living at the same depths, and these differences can be interpreted in terms of different locomotory and feeding habits among the species. Another major contributor to the level of glycolytic activity in fish muscle is body size. Somero and Childress (1980) showed that the activities

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of LDH and PK increased significantly with increasing body size within a species, while enzymes of aerobic metabolism (citrate synthase [CS] and malate dehydrogenase [MDH]) typically decreased in larger individuals of a species. The increased glycolytic capacity per gram muscle in larger individuals of a species is regarded as a mechanism for maintaining a constant capacity of burst swimming, measured in body lengths swum per unit time, in all sizes of fish of a species. Two additional contributors to muscle enzyme activities are condition and dietary influences. For example, muscle LDH activities in field caught anchovies (*Engraulis mordax*) were sevenfold higher than activities in muscle of laboratory reared anchovies, a difference which may derive from conditioning (Somero and Childress, 1980). Conditioning effects on fish muscle enzymic activities have also been reported by Johnston and Moon (1980). Dietary influences on muscle enzyme levels may also be significant. Patterson *et al.*, (1974), Jobling (1980) and Moon and Johnston (1980) have shown that starvation leads to alterations in enzymic activity and, in some instances, in levels of the contractile apparatus.

The present study was undertaken to examine the effects of several of the variables known to influence muscle enzymic activities, namely body size, diet and depth of occurrence, on a single teleost species, the sablefish (*Anoplopoma fimbria*). Through study of field specimens and of fish held under controlled conditions in the laboratory we hoped to learn more about the degree of variation in muscle biochemistry that can occur within a species. This information could be useful for developing biochemical indices for gauging the physiological state of field caught sablefish, and these data also might be of benefit in establishing the relative importance of different factors, *e.g.*, body size *versus* diet, in establishing muscle biochemical properties. The variation in biochemical properties observed within a single species also would shed light on the extent to which interspecific comparisons could be valid.

*Anoplopoma fimbria* was selected for this study because of its wide latitudinal and depth distributions, its capacity to survive under widely varying dietary conditions (Sullivan and Smith, 1982), and its suitability for long-term aquarium holding. The sablefish is a benthopelagic species which occurs on the continental slope from the Bering Sea, Alaska, to off Cedros Island, Baja California, Mexico. It occurs in shallow water (down to 50 m depth) at the northern end of its range, and in relatively deep water at the southern end of its range (down to approximately 1500 m off San Diego, California). There is extensive information available in the literature about the life history and food habits of this species throughout its range (Conway, 1967; Phillips, 1969).

For our study, specimens of *A. fimbria* were collected over much of the species' distribution limits: the Bering Sea, off the Queen Charlotte Islands (British Columbia), Monterey Bay (California), and in the Southern California Bight. All of these areas were sampled at the same time of the year (June–July), and specimens also were collected throughout the year off southern California. A wide size range of fish was obtained to investigate size-specific ("scaling") effects on muscle biochemistry. Aquarium studies were conducted with southern California specimens to examine the effect of ration on muscle biochemistry.

Our results indicate that the biochemical properties (enzymic activity, and protein, lipid, and water contents) of both white skeletal muscle and, to a lesser extent, liver are strongly affected by ration. Seasonal and latitudinal variations in muscle biochemistry seem explainable largely in terms of food availability. Glycolytic enzyme activity in white skeletal muscle is size-dependent. Thus, size-related changes must be segregated in studies of dietary effects.

## Materials and Methods

Sablefish were collected from four sites along the west coast of North America: Bering Sea, Alaska (58°N, 50 m), Queen Charlotte Islands (52°40′N, 90–210 m), Monterey Bay, California (37°30′N, 405 m) and the Southern California Bight Area (two stations: Tanner Basin 32°43′N, 1200 m and San Diego Trough 32°53′N, 1060 m). Fish were collected by trap line, free vehicle set lines (FVSL), and trawls. All fish were measured and weighed, and then muscle and liver tissues were removed and frozen (dry ice) for laboratory analysis. Fish for laboratory holding were collected off San Diego, California at a depth of 468 m, and held as described in Sullivan and Smith (1982). Fish in the laboratory were fed weekly on a diet of chopped squid and mackerel, with records kept of grams ingested by each fish. Five fish were starved, six fish were fed 7% of their wet body weight per week, and six fish were fed 15–18% of their wet body weight per week. After twenty-four weeks in the laboratory, the fish were sacrificed and assayed by the same procedures used for field fish. All muscle samples were taken from a site in the epaxial white musculature behind the gill cover and well above the lateral line. Skin and any red muscle tissue were removed.

Water contents were determined from two 1-gram muscle samples taken from frozen tissue according to the procedure of Sullivan and Somero (1980). Protein concentration of the white muscle was determined using a modified microburet method (Itzhaki and Gill, 1964). Bovine serum albumin was used as a standard. Lipid content of the tissue was determined by a chloroform/methanol extraction and a simple charring method (Marsh and Weinstein, 1966). Tripalmitin was used as a standard. All values are expressed as percent of tissue wet weight.

For the assays of enzymic activity, tissue samples were dissected while frozen, weighed, added immediately to 8 volumes of homogenization buffer (10 m*M* Tris-HCl, pH 7.5 at 10.0°C) at ice bath temperatures (0–4°C), and homogenized in conical ground glass-surfaced homogenizers ("Duall type 23"; Kontes Glass Co., Vineland, New Jersey, USA) driven by hand. The homogenates were centrifuged at 2500 × *g* for 15 minutes and the supernatant fractions pipetted into test tubes, avoiding any superficial lipid layer, and used without additional purification. Further dilution of the homogenates was not necessary.

Activities of LDH and PK in white muscle, and MDH and CS in the liver were measured at 10.0°C (±0.2°C) using freshly prepared homogenates according to the methods of Somero and Childress (1980). Substrate and cofactor concentrations were adjusted to give optimal reaction velocities. All enzyme activities are expressed in international units (μmoles substrate converted to product per minute) per gram of wet (or when noted, dry) weight at 10.0°C. Most discussion of enzyme activities refers to values based on activity per gram of wet weight. This seems most appropriate for estimating the metabolic potential of the tissue. However, activities per gram dry weight are used to factor out the variability in water content of the muscle tissue when examining the scaling effect of glycolytic enzymes with increased size.

## Results

Because the specimens used in this study ranged in weight from 430 g to 3600 g, and in forklength from approximately 40 cm to 80 cm (see Fig. 1), we examined possible size-related ("scaling") relationships between body size and glycolytic enzyme activity. To this end we plotted LDH (Fig. 1) and PK (Fig. 2) activities as a function of forklength for all southern California specimens, the largest group of sablefish used in our studies.

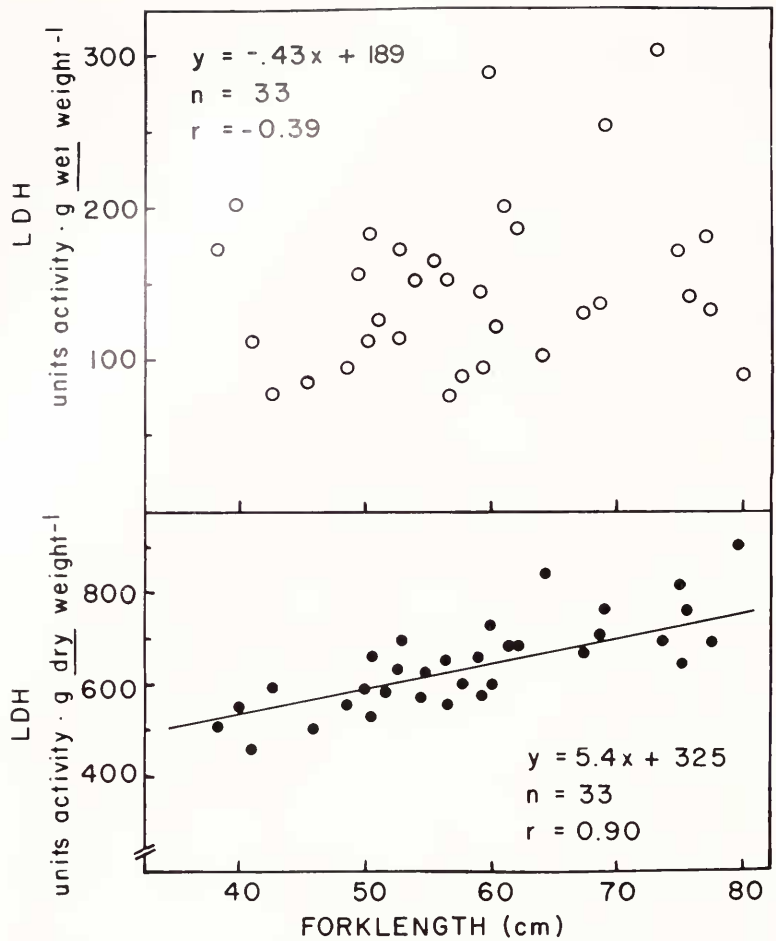


FIGURE 1. A) Lactate dehydrogenase (LDH) activity per gram wet weight in white skeletal muscle of *Anoplopoma fimbria* collected off southern California *versus* forklength. The equation generated by a linear regression is given, with the regression coefficient. B) LDH activity per gram dry weight for the same *Anoplopoma fimbria versus* forklength. The equation generated by a linear regression is given.

Forklength was used rather than body mass because of the greater accuracy in measuring length at sea. Fish caught by FVSLs often retained large quantities of water in their guts, making weight measurements even less reliable. LDH activity *versus* forklength for 33 fish collected off southern California is plotted in units of activity per gram wet weight and per gram dry weight (Fig. 1). The data encompass the full range of sizes studied and include data on individuals collected at different times of the year. LDH activity per gram wet weight does not correlate strongly with forklength ($r = -0.39$). However, converting all the LDH activities to units of activity per gram dry weight yields a strong positive correlation between enzyme activity and forklength ($y = 5.4x + 325$; $r = 0.90$). Similarly, when expressed in terms of units of activity per gram dry weight, PK activity also scales strongly with body size (Fig. 2). The scatter noted in enzymic activities expressed in terms of gram wet weight of tissue is largely a reflection of variation in water content among specimens; water content of white muscle ranged from 62% to 91%, but showed no systematic

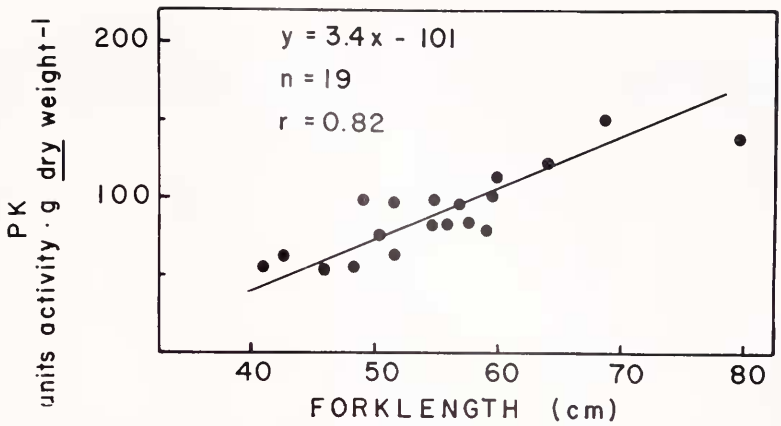


FIGURE 2. Pyruvate kinase (PK) activity (units per gram dry weight) *versus* forklength for *Anoplopoma fimbria* collected off southern California. The equation generated by a linear regression is given, with the regression coefficient.

variation with body size (multiple regression analysis). Thus, while differences among individuals in muscle water content contribute to the variation in enzymic activity (expressed per gram wet weight), the only significant trend noted in this analysis is between length and enzymic activity expressed on a dry weight basis. The fact that significant correlations between enzymic activity on a wet weight basis were not found in the sablefish but were found in most other fishes studied may be due to the unusually large variation in water content found in the sablefish relative to other fishes so examined (*cf.* Siebenaller and Somero, 1982; Siebenaller *et al.*, 1982).

For all comparisons of LDH and PK activities in different experimental groups we performed a correction for size-dependence of enzymic activities on the measured enzymic activities. For example, if a sablefish 66 cm in forklength was found to have a muscle LDH activity of 130 units activity per gram wet weight, and to have 82% water in its white muscle, the units of activity per gram dry weight would be 722 ($130 \times 100/18 = 722$). From the linear regression, the LDH activity increases by 5.4 units per gram dry weight for each centimeter increase in length. All fish have been standardized by convention to a 55 cm "reference fish." Thus, correcting the LDH activity of this 66 cm fish to 55 cm involves subtracting 6 units of LDH activity (5.4 units/cm $\times$ 11 cm = 6 units), to yield a value of 716 units per gram dry weight. Converting back to units per gram wet weight, the size corrected LDH activity is 128. All LDH and PK activity measurements were converted back to units per gram wet weight for comparison to values in the literature.

Although the size correction is not large for specimens near the average length (128 compared to original value of 130 units LDH activity per gram wet weight in the example chosen), this correction may be important in comparing fish at two extremes of the size range examined.

Table I gives the muscle water, protein and lipid content, and muscle LDH and PK activities for fish collected from the four locations on the west coast of North America. All fish were collected during the months of June and July, thus removing variation due to seasonal effects. The fish were collected at successively deeper stations in moving from north to south (see Methods). Factors influencing muscle and liver biochemistry could include not only depth *per se*, but also latitudinal differences in food abundance or available prey species. Fish from the three northern stations

TABLE I

*Average muscle water, protein and lipid content, and muscle lactate dehydrogenase (LDH) and pyruvate kinase (PK) activities per gram wet weight (with standard deviations) for* Anoplopoma fimbria *collected at four stations along the west coast of North America*

| Station (sample size) | Muscle composition[a] | | LDH[b] | PK[b] |
|---|---|---|---|---|
| Bering Sea (n = 16) | Water | 77.7 ± 2.7% | 166 ± 59 | 24.2 ± 10.2 |
| | Protein | 15.0 ± 2.8% | | |
| | Lipid | 5.1 ± 3.2% | | |
| Queen Charlotte Islands (n = 27) | Water | 70.7 ± 5.5% | 181 ± 46 | 17.2 ± 6.0 |
| | Protein | 17.0 ± 6.6% | | |
| | Lipid | 9.3 ± 2.7% | | |
| Monterey Bay (n = 8) | Water | 77.8 ± 4.0% | 134 ± 67 | 17.4 ± 9.0 |
| | Protein | 15.1 ± 2.0% | | |
| | Lipid | 3.0 ± 2.0% | | |
| San Diego, CA (n = 26) | Water | 79.0 ± 6.0% | 112 ± 64 | 15.7 ± 10.0 |
| | Protein | 11.3 ± 4.0% | | |
| | Lipid | 6.4 ± 3.0% | | |

[a] Muscle composition is in percent wet weight of tissue.
[b] International units per gram wet weight of tissue, and size corrected (see text).

have significantly lower muscle water content, and higher protein content (one-way ANOVA, $\alpha = 0.05$). The three northern populations also have a significantly higher muscle LDH activity, but there is no significant difference in muscle PK values (one-way ANOVA, $\alpha = 0.05$). The highest LDH activities were in the fish collected off the Queen Charlotte Islands, and there is a decrease in the average LDH activity moving south from this station.

The composition of liver tissue taken from fish collected in June and July in the Bering Sea, off the Queen Charlotte Islands and off San Diego, California, is given in Table II. There is no significant difference in the water content of the liver tissue among the three stations (one-way ANOVA, $\alpha = 0.05$); however, for the fish collected off San Diego the protein content was significantly higher and the lipid content was significantly lower than for fish from the two northern stations. Lipid values were highest in the fish collected off the Queen Charlotte Islands. The variability in water content of the liver tissue was much lower than that of the white muscle tissue.

TABLE II

*Proximate analysis of liver tissue from* Anoplopoma fimbria *collected in the Bering Sea, off the Queen Charlotte Islands, British Columbia and off San Diego, California*

| Station (sample size) | Percent water | Percent protein | Percent lipid |
|---|---|---|---|
| Bering Sea (n = 10) | 63.9 ± 4.5 | 16.3 ± 3.0 | 15.5 ± 2.6 |
| Queen Charlotte Is. (n = 10) | 55.0 ± 4.5 | 21.6 ± 5.6 | 18.1 ± 4.1 |
| San Diego, CA (n = 17) | 59.3 ± 5.4 | 23.1 ± 3.5 | 10.4 ± 2.9 |

Percent wet weight of water, lipid and protein is given with the standard deviation. All fish were collected in the summer months of June and July.

TABLE III

*Seasonal changes in white skeletal muscle composition and glycolytic enzyme activities for* Anoplopoma fimbria *collected off San Diego, California*

| Month (sample size) | Muscle composition[a] | | LDH[b] | PK[b] |
|---|---|---|---|---|
| February (n = 14) | Water | 78.0 ± 2.4 | 102 ± 31 | 11.3 ± 3.6 |
| | Protein | 13.0 ± 3.1 | | |
| | Lipid | 5.0 ± 1.5 | | |
| August (n = 12) | Water | 71.2 ± 1.8 | 158 ± 64 | 17.6 ± 5.7 |
| | Protein | 15.0 ± 1.0 | | |
| | Lipid | 12.0 ± 3.2 | | |
| December (n = 16) | Water | 76.1 ± 3.6 | 149 ± 65 | 16.2 ± 5.3 |
| | Protein | 11.0 ± 3.2 | | |
| | Lipid | 10.0 ± 3.1 | | |

Fish collected in the months of February, August and December were assayed separately.

[a] Average percent wet weight of water, protein and lipid in the white muscle is given with standard deviation.

[b] International units activity per gram wet weight (corrected for size).

After making size and latitudinal comparisons of muscle composition and enzyme activities, fish collected at the San Diego site throughout the year were examined for seasonal changes in muscle biochemistry. Table III lists the white muscle water, protein and lipid contents, and muscle LDH and PK activities per gram wet weight, size corrected, for fish collected in February, August, and December. The water content in August fish is significantly lower than in fish collected in December and February (one-way ANOVA, $\alpha = 0.05$) and the lipid content is significantly lower in February fish. The white muscle LDH activity is also significantly lower in the fish caught in February; there is no difference in the muscle LDH levels between fish caught in August and in December. There is no significant difference in muscle PK activities among fish caught at different times, but the average PK activity value is lowest for fish caught in February.

To assess the role of diet in both the seasonal and geographic variation of muscle composition and glycolytic enzyme activities of field-caught fish, 17 sablefish were held in the laboratory for 24 weeks to examine dietary-induced changes in muscle, liver and gonad composition, and muscle and liver enzyme activities. Table IV presents the results of this experiment. Three dietary treatment groups, starved, half-ration and full-ration, were used. Enzyme activities and tissue composition values were averaged within groups. Starved fish had significantly higher water content, and lower lipid and protein content in muscle than half- and full-ration fish (one-way ANOVA, $\alpha = 0.05$). There was no statistical difference in any parameter for full and half-ration fish (Student's t, $P = 0.05$). Starved fish have significantly lower muscle LDH and PK activities, but do not differ significantly from fed fish in liver MDH and CS activities or liver protein content.

Although there were no differences in the biochemical parameters of the muscle, liver and gonad of full and half-ration fish, half-ration fish lost weight during the experimental period, while the group of fish on a full-ration gained an average of almost 300 g. Growth rates in laboratory full-ration fish were 25% higher than known field growth rates (Sullivan and Smith, 1982). Starved fish not only lost weight, but suffered loss of muscle protein and lipid, and had higher water contents in liver and muscle tissues. There was no difference in the composition of gonad tissue between

TABLE IV

*Enzyme activities and tissue composition for* Anoplopoma fimbria *kept in the laboratory for 24 weeks on variable rations*

| | Starved n = 5 | Half n = 6 | Full n = 6 |
|---|---|---|---|
| Average Ingestion | | | |
| Rate (g/wk) | 0 | 59 ± 23 | 154 ± 45 |
| % Ration[a] | 0 | 5.0 | 10.2 |
| *White Muscle*[b] | | | |
| Water | 81.8 ± 0.9 | 73.6 ± 1.1 | 71.6 ± 1.7 |
| Protein | 10.0 ± 0.6 | 12.5 ± 1.7 | 11.6 ± 1.4 |
| Lipid | 2.0 ± 0.8 | 11.6 ± 1.9 | 15.2 ± 2.7 |
| Lactate Dehydrogenase[c] | 46.2 ± 22 | 146 ± 36 | 177 ± 27 |
| Pyruvate Kinase[c] | 7.1 ± 4 | 25 ± 13 | 27 ± 5 |
| *Liver*[b] | | | |
| Water | 78.9 ± 1.9 | 64.1 ± 7.9 | 67.6 ± 8.4 |
| Protein | 14.2 ± 2.8 | 19.3 ± 3.1 | 14.7 ± 3.4 |
| Lipid | 3.0 ± 1.6 | 13.0 ± 4.2 | 13.4 ± 3.1 |
| Malate Dehydrogenase | 133 ± 32 | 155 ± 55 | 141 ± 41 |
| Citrate Synthase | 2.1 ± 0.5 | 2.1 ± 0.6 | 2.0 ± 0.6 |
| *Gonad*[b] | | | |
| Water | 85.9 ± 0.8 | 83.5 ± 3.2 | 82.5 ± 1.7 |
| Protein | 6.8 ± 0.7 | 5.7 ± 2.6 | 9.3 ± 1.2 |
| Lipid | 1.2 ± 0.6 | 3.2 ± 1.1 | 3.9 ± 1.2 |
| Average Initial Weight | 1117 grams | 1348 grams | 1220 grams |
| Average Final Weight | 1000 grams | 1197 grams | 1505 grams |

All values are averaged for each of the three treatment groups.

[a] Fish were fed weekly either a half ration (5–7% of wet body weight) or a full ration (15–17% wet body weight).

[b] Percent wet weight of water, protein, and lipid are given for white skeletal muscle, liver, and gonad with standard deviations.

[c] Muscle glycolytic enzyme activities are size corrected.

the groups. Gonadal tissue made up less than 2% of the total body wet weight in all fish.

The relationship between muscle LDH activity per gram wet weight (size corrected) and ration was further examined by plotting the enzyme activities from individual fish from the laboratory experiment against the average percent ration (percent of wet body weight ingested per week) ingested during the 24-week period (Fig. 3). Though the sample size is small, there is a positive correlation between ration and LDH activity. Both a linear regression and non-linear logarithmic curve were fitted to the data. The logarithmic curve ($y = 58.6 + 106 \log x$) gave the best fit ($r = 0.84$).

## DISCUSSION

The relationship between the weight specific oxygen consumption rate and body weight of the sablefish has been determined from laboratory studies (Sullivan and

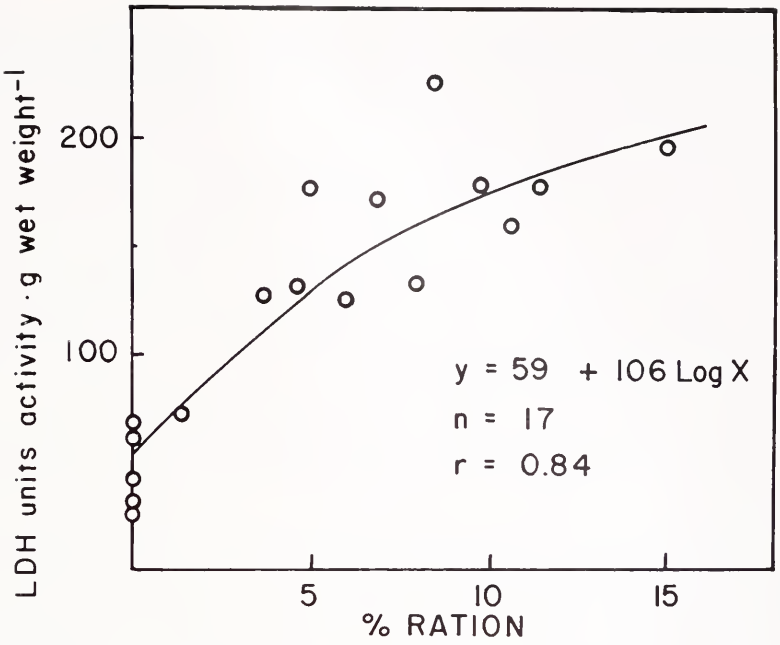


FIGURE 3. Average % ration (percent of wet body weight ingested per week) *versus* white muscle LDH activity per gram wet weight, size corrected for 17 *Anoplopoma fimbria* held in the laboratory for 24 weeks. The logarithmic curve was drawn from the equation y = 58.6 + 106 log x. The regression coefficient (r) is 0.84.

Smith, 1982). The exponent of the equation $\dot{V}_{O_2} = aM^b$ where $\dot{V}_{O_2}$ is the weight specific oxygen consumption, a is a constant, and M is body mass is −0.28. This exponent is not significantly different from −0.26, the scaling coefficient observed for weight specific oxygen consumption for different sized animals (Hemmingsen, 1960; Schmidt-Nielson, 1975). In contrast, the scaling coefficient b for the weight specific LDH activity per gram dry weight of muscle is 0.66. That is, the LDH activity per gram dry weight *versus* forklength data can be fit to a power curve, generating the equation $y = 42x^{0.66}$ where y is LDH activity per gram dry weight and x is forklength. Obviously, the scaling of LDH activity per gram dry weight differs significantly from the scaling of oxygen consumption per unit weight. Somero and Childress (1980) attributed the positive scaling of glycolytic enzymes in other marine teleost species to increased power demands for burst swimming by larger fish of a species. The increase in glycolytic enzyme activity with increasing body size in many of the fishes studied matches closely the predicted increase in swimming power needed to maintain a constant relative burst swimming ability, measured in body lengths swum/unit time over a range of sizes for a given species. Observations of sablefish from submersibles indicate that this species is capable of very fast bursts of swimming when startled by light or disturbances (Sullivan, personal observations). The finding of fast-swimming pelagic organisms, *e.g.*, squid, in sablefish gut contents (Conway, 1967) likewise argues for a robust swimming ability by this fish. Furthermore, the absolute amount of glycolytic activity in sablefish muscle is high, *i.e.*, greater than 100 units LDH activity per gram wet weight relative to other deep-living fishes (*i.e.*, lower than 60 units LDH activity per gram wet weight) examined (Sullivan and Somero, 1980). Thus, selection for a relatively high and size-independent burst swimming ability in sablefish may account for the observed scaling

of LDH and PK activities in white skeletal muscle. Because of the strong scaling of LDH and PK activities per gram muscle with body size (Fig. 1), it is important to correct for the effect of body size in studies where another experimental variable, *e.g.*, diet, capable of affecting muscle enzymic activity is being examined. This correction was made in all cases in our study.

Partitioning the variation in LDH and PK activities to other factors than size led us to examine, first, latitudinally separated sablefish populations which have different depths of occurrence. Latitudinal and/or depth effects appear to have some influence on the activities of these enzymes (Table I). For sablefish collected during the summer months, the mean LDH activity per gram wet weight of muscle was 181 for fish caught off the Queen Charlotte Islands. In contrast, the LDH activity per gram wet weight muscle for fish caught off San Diego was 112; this difference was found to be significant (student's t, $\alpha = 0.05$).

Considering the low lipid content of the muscle and liver tissues of southern California fish, and the large change in muscle glycolytic enzyme activities induced by laboratory starvation, it is most likely that differences seen in the latitudinal comparison of muscle biochemistry in sablefish are induced by dietary rather than depth differences.

Dietary differences may also account for the seasonal changes observed in sablefish muscle biochemistry (Table III). For sablefish collected from the same station off southern California at different times of the year, a change in the muscle composition and enzyme activities is seen at times corresponding to changes in prey availability. Information collected by Conway (1967) on the stomach contents of fish collected throughout the year suggests seasonal changes in prey availability and feeding habits. In February, there is low abundance of two prey species, the fish, *Sebastolobus alascanus*, and the squid, *Loligo opalescens;* ophuiroids and salps are found in stomach samples at this time (Conway, 1967). In February, the lowest LDH activities were observed for sablefish white muscle, along with low muscle lipid content. In August, the young of the year of *S. alascanus* are available as prey items, and in December, many squid are spawning in the submarine canyons. Thus, during these two months, there appears to be a higher abundance of two common prey items (Conway, 1967), and the greatest muscle LDH activities are seen for sablefish at this time. These high muscle LDH activities can be viewed as an effect of an increased ration size or feeding frequency and as an adaptation for increasing the fish's swimming capacity, *i.e.*, its ability to obtain the fish and squid captured at this season.

To analyze further the dietary contribution to muscle enzyme activities, sablefish were kept in the laboratory on various ration sizes and sacrificed after 24 weeks. Compositional analysis of liver, muscle and gonad tissue shows that the muscle is the most responsive tissue to various rations (Table IV). The muscle LDH and PK activities of starved fish were on an average 20% and 25%, respectively, of the activities of fed fish. Muscle water content was significantly higher and lipid content was significantly lower in starved *versus* fed fish.

Jobling (1980) found that in starved plaice (*Pleuronectes platessa*) the muscle tissue was first depleted of glycogen and lipid stores, then the liver was seen to decrease in lipid content. Loss of integrity of liver tissue (higher water content, lower protein and lipid content) was frequently followed by death in starved plaice (Jobling, 1980). It was not possible to assay for glycogen in sablefish tissues since many of the field caught fish struggle vigorously on the FVSLs, and fish were not killed quickly enough to preserve tissue metabolite levels. Patterson *et al.* (1974) noted that plaice serially slaughtered during starvation suffer a loss of integrity in muscle

tissue first, and that white muscle contractile proteins are preferentially utilized by the fish during starvation. With starvation, liver lipid stores are also depleted in sablefish, but there appears to be no change in liver oxidative enzyme activities between starved and fed sablefish. Thus, the activities of liver enzyme are preserved during dietary changes as well as during depth-related changes. Muscle glycolytic enzyme activities, muscle water content, muscle lipid content and liver lipid content appear to be the most informative parameters reflecting the dietary history of the fish.

On the basis of laboratory experiments, one can speculate on the relative ration sizes of field caught fish. For example, fish collected off the Queen Charlotte Islands have the highest average muscle LDH and PK activities, muscle lipid content and liver lipid content. Their ration levels may be higher than the 15% ration (percent wet body weight eaten per week) fed laboratory fish as judged from the higher enzyme activities and lipid contents of muscle and liver. However, laboratory experiments do not take into account energy expended in swimming activity, since fish in the aquarium were kept in confined areas to minimize activity. In light of the laboratory experiment results, the magnitude of change seen in muscle and liver biochemical parameters between northern and southern populations of sablefish could easily be explained by dietary differences, or depth-related changes in food abundance. There is a very strong positive correlation between muscle LDH activity and ration size (Fig. 3) suggesting that this relationship may follow a predictable trend much like other effects of ration on growth and composition. More experiments are necessary to determine the exact nature of the correlation (logarithmic *versus* linear), but the ration size could possibly be determined from muscle enzyme activity information.

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